

## A COMPARISON OF GROUP MERIT SELECTION AND RESTRICTED SELECTION AMONG FULL-SIB PROGENIES OF SCOTS PINE

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### ABSTRACT

Twenty-tree selections were drawn from a 26-year-old full-sib population of Scots pine (*Pinus sylvestris* L.) trees mated according to a partial diallell scheme, in a comparison of 'group merit selection' (GMS) and 'restricted selection' (RS) based on individual breeding values for tree height. In GMS, the selection criterion to be maximised was the group merit (GM), which is equal to the average breeding value of all selected individuals, minus their group coancestry adjusted by a weighting factor expressing the loss of average breeding value per unit increased coancestry. In RS, the maximum number of contributions per parent was restricted. GMS showed a considerable advantage over RS, giving higher average breeding values at any given final status number. Thus, GMS maintained a larger effective population size than RS at any given level of gain. When RS was used, with a maximum of two contributions per parent, a status number of 14 was obtained. Employing GMS, adjusted to give the same status number, resulted in 5.2 % greater average breeding value, with respect to height.

**Key words:** BLUP, breeding population, group coancestry, individual breeding value, group merit selection, *Pinus sylvestris*, restricted selection

### INTRODUCTION

In order to fulfil the growing demand for wood products in a world with declining forest area, it is desirable to use the best-bred materials in reforestation (ZOBEL & TALBERT 1984; PALMÉR & DANELL 1992). However, forest trees are not only regarded as wood producers but also as a gene resource for future biological evolution. Thus, a good method for advancing generations of breeding populations is required, in order to get a substantial genetic gain yet limit the loss of genetic diversity.

The method of restricted selection (RS) can be used to limit the loss of genetic diversity (WEI 1995). Recently, however, additional selection methods have been proposed in which both the breeding value and genetic relationships among members in the selected population are considered. BRISBANE & GIBSON (1995), for instance, regarded the balance between genetic gain and relationship among selected individuals as important in order to achieve gain with minimal inbreeding. Similarly, LINDGREN & MULLIN (1997) considered low group coancestry combined with high gain to be desirable goals, and proposed a 'group merit selection' (GMS) method. GMS is a means of group selection based on assessing the contribution of each individual

to the overall group performance and coancestry. The group with the highest group merit (GM) is then selected.

LINDGREN & MULLIN (1997) formulated a selection algorithm, in order to improve the possibility of maximising GM, which they applied to simulated progenies of single-pair matings, and ZHENG *et al.* (1997) used the same algorithm for clonally replicated material. However, both of these previous studies used materials that were small in terms of number of relationships and trees compared to the number of individuals that generally exist in real breeding populations.

The purpose of this study was to investigate whether GMS is a feasible and practical method to apply in a more typical breeding situation.

### MATERIAL

The 26-year-old Scots pine (*Pinus sylvestris* L.) progenies of 52 plus trees, grafted in a Swedish seed orchard<sup>1</sup> were studied. The parents were mated in a partial diallell scheme, approximately according to KEMPTHORNE & CURNOW (1961), where 202 crosses (out of 212 planned) were successful (Fig.1). The progeny test planta-

<sup>1</sup> Identification at SkogForsk: S23FP1412 Domsjöänget

**Table 1. Basic data and genetic parameters concerning tree heights (dm) measured in the progeny test plantations.**

Number of trees ( $N$ )	4960	
Mean value ( $\bar{y}$ )	70.6	(min = 23, max = 105)
Standard deviation ( $\sigma_y$ )	12.2	
Estimated		
phenotypic variance ( $\sigma_p^2$ )	149.19	
additive genetic variance ( $\sigma_A^2$ )	29.61	
dominance genetic variance ( $\sigma_D^2$ )	15.36	
narrow-sense heritability ( $h^2$ )	0.198	
broad-sense heritability ( $H^2$ )	0.301	
Mean of estimated		
parent breeding values	0	(min = -9.24, max = 9.52)
offspring breeding values	0.14	(min = -11.73, max = 10.44)

tion<sup>2</sup> was established in 1971 at latitude 64°18' N, longitude 19°34' E, and 300 m elevation in northern Sweden. With about 40 sibs per family, 8160 seedlings were planted entirely randomly, and subsequently individually mapped, as 'single-tree plots' at two-meter square spacing.

It is planned that the orchard clones and their

progeny will serve as one of the sources of founders for the 24 sub-populations of the new Swedish Scots pine breeding program (WILHELMSSON & ANDERSSON 1995). At the most recent measurement in September 1997, 5251 living trees remained. In this study, the heights of 4960 healthy trees were considered (mean and standard deviation are shown in Table 1).

## METHODS

### Genetic parameters and parent breeding values

The phenotypic value ( $P$ ) of an individual tree is assumed to be described by the biological model equation  $P = A + D + E$ , where  $A$  is the additive genetic value (or breeding value, BV),  $D$  is the genetic dominance deviation and  $E$  is the residual deviation where environmental effects dominate. Epistatic, maternal, reciprocal, and all other effects are assumed to be zero or negligible and included in  $E$ . The corresponding variances are thus expressed as  $\sigma_p^2 = \sigma_A^2 + \sigma_D^2 + \sigma_E^2$ . Narrow-sense and broad-sense heritabilities were estimated according to  $h^2 = \sigma_A^2 / \sigma_p^2$  and

$H^2 = (\sigma_A^2 + \sigma_D^2) / \sigma_p^2$ , respectively. (FALCONER & MACKAY 1996).

In order to eliminate as much environmental distur-

bance as possible in the subsequent evaluation, the experimental area was subdivided into 70 equal-size, square blocks. The block size was chosen with respect purely to the distribution of observations per block, utilising previous experience from similar situations (ERICSSON 1997, 1999; WILLIAMS & FU 1999). The phenotypic values were approximated from the linear model equation  $y_{ijkl} = b_i + a_j + a_k + f_{jk} + e_{ijkl}$ , where  $y_{ijkl}$  is the phenotypic value of an individual tree, the fixed effect of block  $i$  ( $i = 1, \dots, 70$ ), the random effect of mother  $j$  ( $j = 1, \dots, 30$ ), the random effect of father  $k$  ( $k = 24, \dots, 52$ ), the random effect of the full-sib family with mother  $j$  and father  $k$ , and the residual effect of an individual tree, including environmental and residual genetic effects ( $l$  varies from 1 to 40). All model terms were assumed to be independent and their variances were expressed as  $\sigma_y^2 = 2\sigma_a^2 + \sigma_f^2 + \sigma_e^2$ , where  $\sigma_a^2$  is the parental variance (assumed to be equal for mothers and fathers),  $\sigma_f^2$  the family variance, and  $\sigma_e^2$  the residual variance.

Best linear unbiased predictors (BLUPs) of the parent effects were obtained through resolving the mixed model equations (MME) corresponding to the statistical model. In the MME, the variances  $\sigma_a^2$ ,  $\sigma_f^2$ , and  $\sigma_e^2$  were replaced by the corresponding restricted maximum likelihood (REML) estimates. All predictors and estimates were computed with the SAS Mixed procedure (LITTELL *et al.* 1996). The phenotypic variance (i.e. the variance of phenotypic values of individual trees,  $y_{ijkl}$ ) was estimated assuming  $\sigma_p^2 = \sigma_y^2$ . Since the BV of parent  $i$  is  $A_i = 2$ , the additive variance was estimated according to  $\sigma_A^2 = 4\sigma_a^2$ . The dominance variance was estimated utilising  $\sigma_D^2 = 4\sigma_f^2$  according to various authors, such as BECKER (1992).

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$$\bar{B}\bar{V} = \frac{1}{n} \sum_{i=1}^n BV_i \quad [2]$$

and

$$\Theta = \frac{1}{n^2} \sum_{i=1}^n \sum_{j=1}^n \theta_{ij} \quad [3]$$

respectively, where  $n$  is the number of selected individuals and  $\theta_{ij}$  the coancestry between individuals  $i$  and  $j$  with 'self coancestry'  $\theta_{ij} = 0.5$  when  $i = j$ . All parents were assumed to be unrelated and non-inbred. Thus  $\theta_{ij} = 0.25$  when  $i$  and  $j$  are full-sibs,  $\theta_{ij} = 0.125$  when they are half-sibs, and  $= 0$  if  $i$  and  $j$  are unrelated.

The group merit is a criterion for group merit selection. The constant  $c$  has the same dimension as the breeding value, and thus GM may be considered a reduced breeding value. However, GM is not an acceptable criterion for measuring breeding progress, which still must be measured in terms of increased  $\bar{B}\bar{V}$  for performance and change in  $\Theta$  or  $N_s$  for coancestry. GM has relevance within the base population ('meta-group') from which selection is being made. GM may still be computed for any selected subset from the same base population in order to compare, for example, GM for varied selection methods. Useful  $c$  values must be found empirically, and may take any positive value. In a new selection situation, the initial search for the best subset may include  $c$  values spanning several orders of magnitude or a similar range.

For a certain, specific  $c$  value, maximum GM could be determined by an exhaustive search of all possible sets of  $n$  individuals. However, in a tested population of size  $N$  there are  $(N!)/((N-n)!n!)$  combinations of  $n$  individuals, so in this study, with a population of  $N = 4960$ , setting  $n = 20$  generates a very large number of possible permutations. There is no known general procedure to find the best set or to validate a suggested best set without testing all combinations, which in most real situations is practically impossible. Instead, an iterative search algorithm can be designed with a high probability of finding the best or near-best set. Similar techniques have been employed in stepwise regression procedures (DRAPER & SMITH 1966), and proposed recently for GMS (LINDGREN & MULLIN 1997; ZHENG *et al.* 1997). In this work, the following modification, based on the last two studies listed, was designed for selecting  $n$  out of  $N$  individuals with a given weighting constant ( $c$ ):

1. Define an initially empty ( $n = 0$ ) set of trees, the *selects*, and a set of candidates for selection, initially including all  $N$  trees, called the *remainder*.

2. Select the individual in the remainder which, when moved to the selects, will maximise their GM, and move it to the selects. Repeat this step until  $n$  has

reached the desired number.

3. Move one individual from the selects to the remainder. The selects now consist of  $n - 1$  trees. Then take the best from  $(N - n) + 1$  trees in the remainder to replace the select removed. In most cases the removed individual will qualify to be restored, but it may occasionally be replaced. Repeat this step until every  $n$  individual has been removed once (however, a replaced individual is not considered repeatedly). The set with theoretically maximal GM has now been obtained. In order to obtain different selections by GMS to compare with RS, penalty constants from 0 to 600, in increments of 20, were used.

### Restricted selection

Adopting the same terminology as above, the RS method implies successive selection of the individual with the highest breeding value from the remaining set. However, no parent is allowed to contribute more than a pre-set maximum number of times (the restriction number, RN). If a parent of a tree is already represented RN times, the candidate individual is rejected and the next in rank is considered for the selects. When the  $n$ -tree population size is reached, GM,  $\bar{B}\bar{V}$ , and of the selects are calculated for comparison with corresponding results from GMS.

With RN = 1, the maximum possible  $n$  value is 24, set by the crossing-scheme. Since it was planned to compare GMS with RS from RN = 1 to 5,  $n = 20$  was chosen as a convenient number for this study.

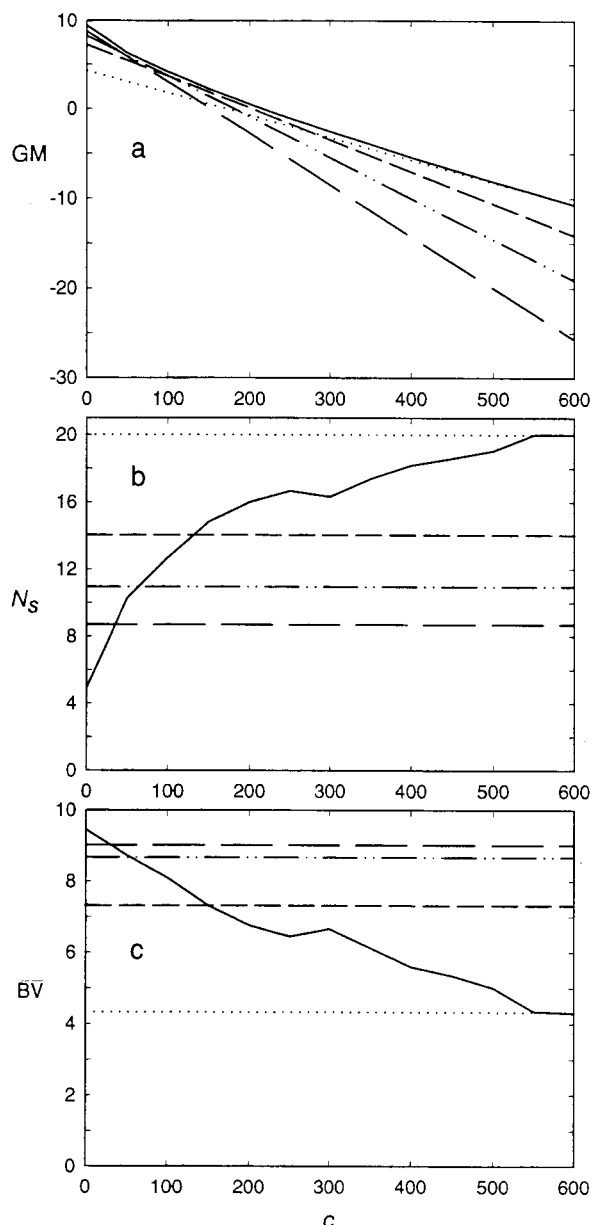
### Computing

In order to perform GMS and RS on the experimental material, a new computer program was developed to carry out GMS with varying  $N$ ,  $n$ , and  $c$  parameters, as well as RS with varied  $N$ ,  $n$ , and RN.

## RESULTS AND DISCUSSION

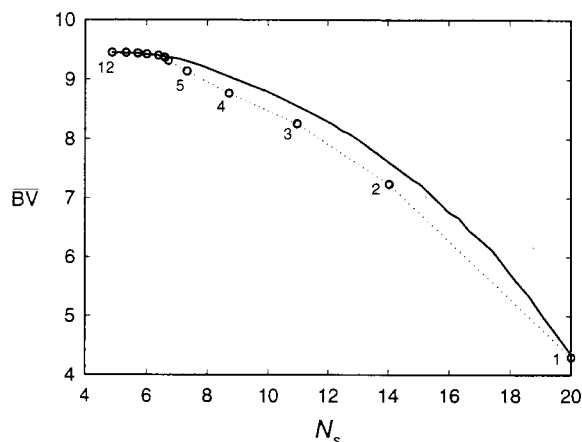
### Group merit

The GM values obtained by the two methods after selecting 20 trees out of the 4960 were compared at different weighting constants. At  $c = 0$ , where relatedness does not affect the selection decision, the group merit is equal to the group breeding value ( $GM = \bar{B}\bar{V}$ ). When the weighting constant was increased, the GM decreased. Minimal group coancestry was reached at  $c = 550$ . Above this value, changes in GM were no longer due to changes in the average breeding value or group coancestry but only in  $c$ . Fig. 2a shows that in most cases GMS gives a higher GM, except at very



**Figure 2a-c.** Group merit (GM), status number ( $N_s$ ) and average breeding value ( $\bar{BV}$ ) at various weighting constants ( $c$ ) for 20 trees selected out of 4960 by GMS (—) and RS with  $RN = 1$  (.....),  $RN = 2$  (— — —),  $RN = 3$  (— · — · —), and  $RN = 4$  (— — —). For GMS and RS, equal  $N_s$  and  $\bar{BV}$  were obtained for  $RN = 1$  at  $c \approx 550$ ,  $RN = 2$  at  $c \approx 150$ ,  $RN = 3$  at  $c \approx 50$ , and for  $RN = 4$  at  $c \approx 30$ .

high weighting constants ( $c > 550$ ), where RS with  $RN = 1$  is equivalent. Since all individuals come from unrelated and non-inbred parents, the minimum group coancestry possible for GMS is equal to what is obtained with RS when selection is restricted to not more



**Figure 3.** Average breeding value ( $\bar{BV}$ ) as a function of status number ( $N_s$ ) for GMS (curve) and for RS at  $RN=1, \dots, 12$  (circles and figures). At  $RN = 2$  ( $N_s \approx 14$ ), the  $\bar{BV}$  obtained by GMS is 5.2% ( $\approx 0.4$  dm) superior to the  $\bar{BV}$  obtained by RS. The differences between the two methods were most notable between  $N_s \approx 8$  and 15.

than one individual per parent. The situation is different if the parents of the candidates are related, which is more likely in advanced generations. Whenever related parents are involved, GMS will always give a higher GM at any specific weighting constant (OLSSON *et al.* 2000b).

GMS is also superior to RS when GM is considered at equal status number. At  $n = 11$  and  $c = 60$ , for instance, GMS of 20 trees gives 5.4% more gain than RS (Table 2a-b).

### Status number/group coancestry

In order to compare RS with GMS, was also computed for completed RS with varying  $RN$ , using equation (3) and  $N_s = 1/(2\Theta)$ . Fig. 2b shows status numbers obtained with both methods at various weighting constants. For GMS,  $N_s$  increases with increasing  $c$  and reaches its maximum value, equal to the census number (20), at  $c = 550$ . If any of the selected trees are related, the maximum status number is smaller than the census number (OLSSON *et al.* 2000a, b). For RS, the  $N_s$  of the selects is independent of the change of weight but increases with increasing  $RN$ .

In practice, when selection is carried out in order to advance the breeding population into the next generation, the population size is often decided in advance, and suggestions of suitable population sizes have been made (WHITE, 1993).

In GMS, neither  $N_s$  nor  $c$  is used as a direct selection criterion. Different status numbers are obtained, by

**Table 2a–c.** The selects chosen with GMS (a) and RS (b) at  $N_s \approx 11$ . Most individuals in both methods, and their progeny numbers are marked with boldface. The sets of contributing parents may be compared with the 20 best parents (c), sorted by decreasing breeding values, see the footnotes. The GM in both selections is calculated with weighting constant 60.

a				b				c	
GMS with $c = 60$				RS with $RN = 3$				The 20 best parents	
$N_s = 10.81$				$N_s = 10.96$				based on estimated	
$\bar{B}\bar{V} = 8.594$ dm				$\bar{B}\bar{V} = 8.258$ dm				BVs for tree height	
GM = 5.819				GM = 5.520					
representing 16 families with 18 parents				representing 14 families with 17 parents					

Progeny No.	Parent No.			Progeny No.	Parent No.			Parent No.	BV
	BV	1	2		BV	1	2		
2832	10.44	16	43	2832	10.44	16	43	16	9.52
4731	10.29	27	49	4731	10.29	27	49	10	8.81
2733	10.06	16	39	2733	10.06	16	39	49	7.95
2817	9.84	16	43	2817	9.84	16	43	27	7.83
1749	9.58	10	39	1749	9.58	10	39	8	7.60
4747	9.44	27	50	4747	9.44	27	50	43	7.10
1740	9.28	10	39	4722	9.40	27	49	26	5.91
2890	9.26	16	45	1740	9.28	10	39	22	5.74
4618	9.11	26	49	4618	9.11	26	49	23	5.49
3793	8.93	21	49	3669	8.85	21	43	39	5.35
4623	8.86	26	49	1731	8.52	10	38	50	5.07
3669	8.85	21	43	4208	7.43	23	50	21	5.05
1731	8.52	10	38	3835	7.30	21	50	45	4.17
1722	8.36	10	38	3900	7.05	22	45	18 <sup>3</sup>	3.80
4208	7.43	23	50	3880	6.98	22	45	1 <sup>3</sup>	2.84
3900	7.05	22	45	3883	6.70	22	45	11 <sup>3</sup>	2.33
611	6.80	5 <sup>1,2</sup>	27	1178	6.64	8	31 <sup>2</sup>	24 <sup>3</sup>	2.19
1178	6.64	8	31 <sup>2</sup>	1325	6.58	8	37 <sup>2</sup>	38	2.08
1325	6.58	8	37 <sup>2</sup>	1326	6.06	8	37 <sup>2</sup>	9 <sup>3</sup>	1.73
4039	6.56	22	51 <sup>1</sup>	4599	5.61	26	48	51	1.67

<sup>1)</sup> Selected with GMS only (not in Table b).  
<sup>2)</sup> Selected in spite of not being among the 20 best parents (not in Table c).  
<sup>3)</sup> Unselected in spite of being among the 20 best parents (neither in Table a nor b).

putting in different  $c$  values, which describe the ‘status of relationship’ among the selected candidates. In the case when a target is specified beforehand, the corresponding  $c$  value can be found by repeated selection using different  $c$  values until the desired is approached.

**Genetic gain**

Average breeding value versus weighting constant

The genetic gain for the selected group was expressed in terms of average breeding value. For GMS,  $\bar{B}\bar{V}$  decreases with increasing  $c$ , as shown in Fig. 2c together with  $\bar{B}\bar{V}$ 's for RS with varying RN.  $\bar{B}\bar{V}$  reached its minimum value when  $c = 550$  for GMS, and when  $RN=1$  for RS. For RS, the rise in  $\bar{B}\bar{V}$  is approxi-

mately ‘exponential-to-a-maximum’ with increasing RN. The average breeding value obtained with GMS compared with that obtained with RS at equal  $N_s$  (Fig. 3) is notably higher at the points where RN is between 2 and 5 (equality at  $RN=1$  is apparently trivial).

A general understanding of the conditions for which one method is better than the other can be obtained by comparing genetic gain versus weighting constant. However, the issue of how much weighting diversity should be given must be resolved, which can only be done by testing different  $c$  values while considering average breeding value as well as status number and group merit. When selecting for a seed orchard the  $c$  value can be considered equivalent to inbreeding depression in seeds (OLSSON *et al.* 2000a, WILCOX, 1983).

### Average breeding value versus status number

The average breeding value obtained by GMS was never lower than that obtained by RS at corresponding levels of group coancestry. The highest difference in average breeding value between the two methods was obtained at  $N_s = 14$ , where GMS yielded 5.2% more than RS. Nevertheless, selection at status number 11 gave more total genetic gain than at status number  $N_s \approx 14$ . At 14, the average breeding value was 7.24 dm (10.3 %) and 7.62 dm (10.8%) for RS and GMS, respectively. Corresponding average breeding value figures at  $N_s \approx 11$  were 8.26 dm (11.7 %) and 8.57 dm (12.1%), respectively.

The preceding values were for average breeding values with respect to tree height. For volume, the corresponding figures may be even higher, due to the shift from a linear to a cubic scale. The distinction between the methods may also be greater if the RS is balanced, that is, if the selected parents are allowed to contribute exactly equal numbers of offspring.

We have only considered a single trait, and in practice it is usually desirable to combine several traits into an index. However, there is no principal difference between applying any selection method using an index value assigned to each tree rather than a single trait value.

### Selected populations

To compare the selections made by the two methods at the same status number, the census number 20 and status number 11 were chosen, assuming that the latter is sufficient for maintaining genetic diversity. This status number was obtained when  $c = 60$  for GMS and  $RN = 3$  for RS. The value  $c = 60$  means that if coancestry is unity, GM will be 60 units less than the group's mean breeding value. In the trees studied this corresponds to 60 dm in height: almost six times more than the maximum BV deviation from the general mean. Tables 2a–b show the sets chosen by both methods. The average breeding value obtained by GMS was 4.1 % higher than the corresponding value derived by RS.

Table 2 shows there is not much difference among the selected parents or families that were selected by the two methods, and most selected progeny originated from the 20 best parents. This may be a good argument for forward selection, direct from tested individuals, in order to save a generation of time in the breeding program. Of the 20 selected individuals selected by the two methods, 14 (70 %) appeared in both sets, and the parents/families of most of the selected individuals were represented in both sets. Using GMS, 15 out of

the 18 parents of the selected individuals were amongst the 20 best parents. The corresponding figures for RS were 14 out of 17 (Table 2c). Some parents contributed their genes to more than one individual.

This study considered forward selection. An alternative way of breeding is to use this type of progeny test for backward selection. The mean breeding value of the 20 best parents (Table 2c) is 5.11 dm. If only the 11 top ranking trees are chosen, a mean value of 6.94 is obtained ( $N_s = 11$ ). To get a higher genetic gain with backward selection than with 20 GMS forward selected offspring, selection could be restricted to the three highest-ranking parents ( $N_s = 3$ ). Thus, backward selection does not seem to be desirable in this case. However, one option may be to also include the plus-trees, and not just their offspring, among the candidates available for recruitment, as suggested by ZHENG *et al.* (1997).

GMS was superior to RS when genetic diversity was considered, which should always be done in breeding programs. Provided that the pedigree is available, GMS should be a particularly useful tool when selection is carried out in advanced generations with a complex pedigree, and when group coancestry has reached levels that require it to be managed for future generations. If GMS is used repeatedly at every generation turnover, its benefit will be accumulated over generations (ROSVALL & ANDERSSON 1999).

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